

TABLE 2.
Percentage Germination of Uredospores Stored under Various Conditions of Temperature and Relative Humidity.

Relative humidity ..	25%.					50%.					75%.				
	5	10	20	25	30	5	10	20	25	30	5	10	20	25	30
Temperature (°C.) ..															
8 days	+++	+++	+++	++	+	++	++	++	++	+	++	++	++	++	++
15 "	+++	++	++	++	+	++	++	++	++	+	++	++	++	+	+
21 "	+++	++	++	++	+	++	++	++	++	+	++	++	++	+	+
40 "	+++	++	++	+	-	++	++	++	+	-	++	++	+	-	-
54 "	+++	++	++	-	-	++	++	++	+	-	++	++	+	-	-
62 "	+++	++	+	-	-	++	++	++	-	-	++	+	-	-	-
80 "	++	++	+	-	-	++	++	+	-	-	+	+	-	-	-
103 "	++	++	-	-	-	+	+	-	-	-	+	-	-	-	-
116 "	+	+	-	-	-	+	+	-	-	-	-	-	-	-	-
129 "	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

+++ = 50-100% germination. ++ = 5-50% germination. + = less than 5% germination. - = no germination.

uredospores was noted. The longest period for which uredospores remained viable during these tests was 116 days at 5° and 10°C. at relative humidities of 25% and 50%. The shortest period was 21 days at 30°C. at all humidities.

The longevity of uredospores is of great importance in the epidemiology of rust diseases. These spores are specially suited to transport by air currents, but they must be able to remain viable under the conditions existing in the atmosphere if this is to be an effective method of spreading the disease. Many factors are concerned but here only temperature and humidity have been considered. The results show that, at low temperatures and relative humidities up to 50%, uredospores of *P. antirrhini* produced under local conditions are able to remain viable for about four months. Their transport in cool air currents, probably at high altitudes (Gäumann, 1950), would thus constitute a definite hazard to plants quite long distances away.

It is also apparent that uredospores could remain viable for some time under cool conditions in dust in seed samples. Such samples are dry and, unless conditions of very low humidity adversely affected uredospore longevity, as has been found with some rusts (Gäumann, 1950), they would seem to provide an excellent means for rust dispersal. Air transport of seed samples would make this even more effective.

Further discussion of wind and seed transport of uredospores is given under "Epidemiology".

EPIDEMIOLOGY.

In this section will be considered first the possible means by which the fungus was introduced to Australia, and second its spread within the country.

1. Entry of the Disease.

The way in which *Antirrhinum* rust was introduced to Australia is not definitely known. In seasons when locally grown snapdragon seed is in short supply, bulk lots of seed are imported from Europe and America, and small quantities of new varieties are constantly being introduced from both countries. The crop on which the first infection was recorded was grown from European seed. Before the identity of the race present was established, it was therefore thought that the Australian outbreak had a European origin. As race 2, however, has been recorded only in America and Southern Rhodesia, it now seems that the original entry must have been from America. A European origin for the Australian outbreak would seem to be disproved unless race 2 has become established fairly recently in some countries there. No record of snapdragon seed being imported from Africa has been seen.

Examination of many seed samples showed that the majority of overseas seed coming into New South Wales contained rust uredospores and sometimes teleutospores as well. Of 185 seed samples examined, 139 (75%) were found to contain rust spores. The results of these examinations, with the country of origin of the seed, are given in Table 3. A rough estimate of the number of uredospores present in the seed samples, made using a Bausch and Lomb mould counter, showed that, in most samples, there were from $1-2 \times 10^6$ uredospores present per ounce of seed. However, it was not found possible to germinate these spores or to obtain infection on susceptible seedlings with them. Moreover, plants grown from this seed, and from seed dusted with fresh local uredospores, always produced disease-free plants.

In favour of seed transmission are the facts that under dry and cool conditions rust uredospores can remain viable for a considerable time and that air transport of seed could allow seed to be introduced within a couple of months of harvesting. Under these conditions there seems to be little reason against the production of the disease, for example in a nursery, by the accidental dusting of spores on to snapdragon seedlings when seed was being sown in adjacent beds.

The entry of the rust into other countries has sometimes been attributed to seed transmission, e.g., Sweden (Palm, 1937), South Africa (Bottomley, 1940) and Italy (Preti, 1935), but other workers, after various investigations, have rejected seed transmission (Green, 1941; Hassebrauk, 1937). These latter workers, however, did not seem

to consider the possibility of viable spores, carried in seed, being dusted onto established plants in a nursery area. Baker (1953, personal communication) considered this a distinct possibility and definitely favoured seed transmission.

In the case of the Australian outbreak, evidence against seed introduction are the facts that it was not found possible to germinate the uredospores found in seed samples or obtain infection with them and that, if seed transmission were effective, one would have expected the disease to have been introduced some time ago, considering the large number of uredospores in introduced seed.

Other methods by which this disease could be spread are on cuttings and seedlings, by wind and by spores adhering to clothing. In view of the strict plant quarantine regulations in force in New South Wales it is most unlikely that seedlings or cuttings could have been imported. Wind entry of the disease is unlikely as, at this time, the nearest known source of inoculum was in the Hawaiian Islands, more than 4,000 miles from Sydney. The entry of the disease by spores adhering to clothing is doubtful.

It can thus be seen that the most likely method of entry of this disease was by means of viable uredospores adhering to seed.

TABLE 3.
Results of Antirrhinum Seed Examinations.

Country of Origin.	Number of Samples.		Total Number Examined.	Percentage Containing Spores.
	+	—		
Holland	125	19	144	87
New Zealand	4	24	28	14
United Kingdom	4	2	6	67
Italy	2	—	2	100
France	2	—	2	100
Germany	1	—	1	100
America	1	—	1	100
Tasmania	—	1	1	0
	139	46	185	75

+ = spores present.

— = spores not seen.

Note.—The figure of "100% infection" given in the above table for seed samples coming from Italy, France, Germany and America is a misleading one in view of the small number of samples examined from these countries. Examination of further samples would probably reveal the presence of some without rust spores.

2. *Spread of the Disease in New South Wales.*

After the first outbreak of rust was found in a Sydney suburb it spread rapidly throughout eastern New South Wales. Within four and a half months it had been recorded 100 miles from its source and within a year from its first discovery was widespread in eastern New South Wales.

From a study of the records it has been found that spread in New South Wales occurred in two main ways. These were: (i) primary spread by wind dispersal of uredospores and (ii) secondary spread by the carrying of the diseased seedlings and cuttings from place to place.

(i) *Spread by wind-borne uredospores.*

Wind is one of the most important agents for the dispersal of plant pathogens. With rust fungi, the uredospore stage is well adapted for wind spread and considerable work has been done in tracing the spread by air currents of many of these organisms, especially the cereal rusts. Lambert (1929) showed that evidence exists that uredospores of wheat stem rust may be carried in air currents several hundred miles from their

original source. Wallace (1932), studying the prevalence of various physiologic races of wheat stem rust in the United States in various years, found striking evidence in some years of a south to north migration of rust. This migration was by means of wind-borne uredospores formed early in the season in Mexico and Texas, and carried northward by southerly winds. In western Canada, Craigie (1945) found that the initial inoculum for the production of wheat stem rust consisted largely, if not entirely, of wind-borne spores that originated outside western Canada.

In New South Wales, strong evidence is presented that the initial spread of snapdragon rust was by means of wind-borne uredospores. Text-figure 2 shows the nature of this spread. Zone 1 represents the initial outbreak area of the disease, and Zones 2, 3 and 4 its spread 9 weeks, 15 weeks and 18 weeks after the first outbreak. Text-figure 2 was prepared by marking in the furthest points from the initial outbreak area at which the disease had been recorded at the end of 9, 15 and 18 weeks respectively from the time of the first outbreak and then joining these points up to give the three zones shown.

TABLE 4.
Surface Wind Direction Records at Sydney Weather Bureau for the Period from 1/11/1952 to 28/2/1953.

Wind Direction.	November, 1952.	December, 1952.	January, 1953.	February, 1953.
N. ..	1	0	0	0
S. ..	2	8	9	4
E. ..	7	1	6	10
W. ..	13	3	2	2
N.-E. ..	29	47	40	29
E.-S. ..	13	14	29	23
S.-W. ..	11	10	2	7
W.-N. ..	10	8	2	8
Calm ..	4	2	3	1
Total	90	93	93	84

It can be seen from Text-figure 2 that the main direction of spread of the rust during this period was in a south-westerly direction and only after this did a northward spread to Gosford and the north coast of New South Wales occur. Surface wind direction records at Sydney Weather Bureau have been obtained for this period and are summarized in Table 4. Records are taken three times a day, at 9 a.m., 3 p.m. and 9 p.m., and the table shows the number of records of each wind direction for the period from 1st November, 1952, to 28th February, 1953. It can readily be seen that, in each month, wind was recorded more from a north-easterly direction than from any other; in fact, over the four-monthly period 46% of the records were from the north to east quarter and the prevailing winds for this period are given as north-easterly.

A definite correlation between prevailing wind direction and the initial direction of rust spread in New South Wales is thus seen to exist, and the evidence is strongly in favour of wind-borne uredospores as the primary means by which the disease spread in this State.

From the map it is seen that during the first four months spread was mainly in a south-westerly direction, and in 18 weeks the disease had been recorded 100 miles from its initial focus. Considering the comparatively thin population of snapdragons throughout the area enclosed by Zone 4, this spread is quite rapid and shows the efficiency of the wind-borne uredospores in extending the range of the fungus. From the ninth to the eighteenth week of spread, i.e. from the edge of Zone 2 to the edge of

Zone 4, the rust spread over an area approximately 10 times greater than that which it had covered during its first nine weeks. This indicates that an initial build-up of uredospore inoculum occurred on snapdragons in the Sydney suburban area (Zone 1 and part of Zone 2) during the first nine weeks and later spread in epidemic proportions over a much wider area. The rapid spread and widespread destruction had all the marks of a progressive or spreading epidemic, characteristic of the invasion of a new area by a pathogen (Gäumann, 1950). The severity of the epidemic was increased by the fully susceptible nature of all the host varieties being grown.

(ii) *Spread on diseased plant material.*

Once the disease had become established over a fairly wide area by means of wind-borne uredospores, secondary spread began to occur by the transport of diseased seedlings and cuttings from this area to other parts of the State. Quite often the transported plant material was only very lightly infected and the disease escaped attention, but, when planted out, the disease developed and set up secondary foci of infection from which further wind spread could occur. In this way it was introduced to Cooma in southern New South Wales, about 270 miles from Sydney, and also to other areas. This considerably assisted its spread in Australia. Soon after the Cooma outbreak it was widespread in southern New South Wales.

This vegetative transmission of snapdragon rust hastened its spread by carrying it long distances and allowing it to become established in widely scattered places in a comparatively short time.

3. *Spread of the Disease in Australia.*

By the methods outlined above, snapdragon rust became widespread in eastern New South Wales. Very soon after, spread to other States in Australia occurred and the disease was reported from the southern State of Victoria. Later, in the spring of 1953, it was recorded from Queensland and, in January, 1954, from South Australia. By March it had reached Tasmania, leaving Western Australia as the only State still free of the disease at the time of writing.

The exact method of introduction of the disease to other States is not known but most probably both wind and vegetative spread were concerned. It is known that diseased seedlings were sold in some States and quite possibly they provided foci from which further spread by wind occurred.

4. *Outbreak of the Disease in New Zealand.*

Towards the end of December, 1953, rusted snapdragons were observed in a private garden at Auckland, New Zealand. Brien (1954, private communication) states that no further spread from this area appears to have occurred.

Possible sources of infection include seed and wind-borne uredospores. The question of seed transmission has been discussed in the case of the New South Wales outbreak and similar conclusions were reached in New Zealand. It is possible, however, that uredospores have been carried by wind from Australia to New Zealand and resulted in the outbreak of the disease in that country. Quite often, dust from Australia is deposited in New Zealand, having been carried across by north-west winds, and it would seem quite possible that with the large bulk of uredospore inoculum available in eastern Australia some uredospores would reach New Zealand in air currents. The distance from Sydney to Auckland is about 1,400 miles, but it is not improbable that spores could be carried this distance in air currents.

SUMMARY.

1. Antirrhinum rust, caused by the fungus *Puccinia antirrhini* D. & H. was first recorded in Australia in October, 1952.

2. The race present is similar to or identical with that known in America as race 2 and no varieties have been seen that are resistant to it. Two varieties of *Linaria* inoculated with the rust showed no sign of infection.

3. Locally produced uredospores were found to remain alive for 116 days under conditions of low temperature (5° and 10°C.) and relative humidities (25% and 50%). As temperature and humidity rose, the longevity of the spores decreased.

4. The entry of the rust disease is discussed and it appears that the most probable method of entry was as spore dust in seed samples. At planting time this dust could be blown to nearby plants and infect them. Several points against this hypothesis are discussed.

5. An American origin for the Australian outbreak is tentatively proposed from evidence based on the physiologic race of the rust fungus present.

6. The spread of the disease in Australia is seen to consist of three main phases: (i) primary spread from its initial focus by means of wind-borne uredospores; (ii) secondary spread in New South Wales on diseased plant material; (iii) spread throughout Australia by wind-borne uredospores which were spread from secondary foci of infection established by diseased planting material.

7. The recent outbreak of the disease in New Zealand is mentioned and a possible Australian origin put forward for it.

Acknowledgements.

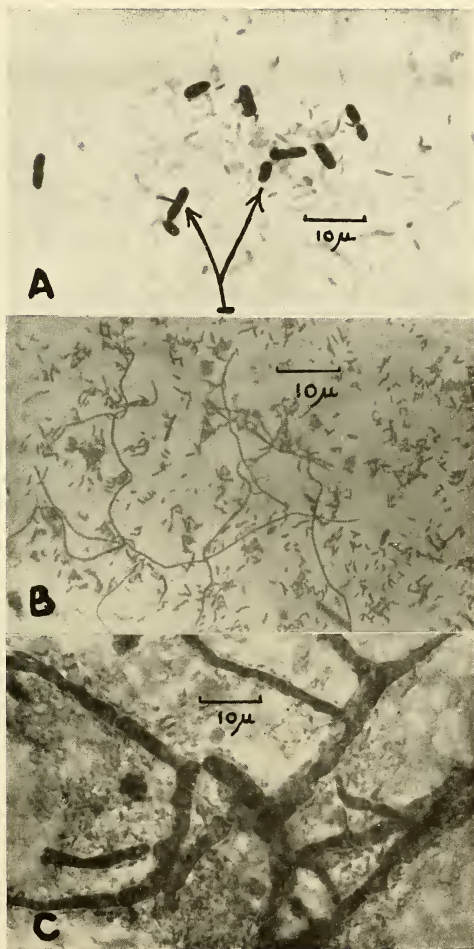
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References.

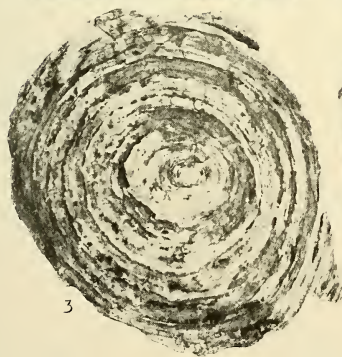
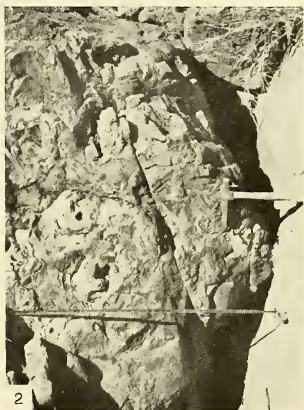
- BLASDALE, W. C., 1903.—On a rust of the cultivated snapdragon. *J. Mycol.*, 9: 81-82.
 BOTTOMLEY, A. M., 1940.—A destructive Antirrhinum disease new to South Africa. *S. Afr. hort. J.*, 2: 17. Abs. in *R.A.M.*, 19: 350, 1940.
 CRAIGIE, J. H., 1945.—Epidemiology of stem rust in Western Canada. *Sci. Agric.*, 25: 285-401.
 DICKSON, B. T., 1921.—Plant diseases of 1920-21. *Thirteenth Ann. Rept. Quebec Society for the Protection of Plants*, pp. 66-67. Abs. in *R.A.M.*, 1: 374-375, 1922.
 DIETEL, P., and HOLWAY, E. W. D., 1899.—*Hedwigia*, 36: 298 (from Blasdale, 1903).
 DIMOCK, A. W., and BAKER, K. F., 1951.—Effect of climate on disease development, injuriousness and fungicidal control as exemplified by snapdragon rust. *Phytopathology*, 41: 536-552.
 DOIDGE, E. M., 1941.—South African Rust Fungi. IV. *Bothalia*, 4: 229-236.
 FIKRY, A., 1937.—Egypt: appearance of Antirrhinum rust in the country. *Int. Bull. Pl. Prot.*, 11: 1.
 ———, 1938.—Rust pustules on roots of Antirrhinum. *Ann. Bot., Lond., N.S.*, 2: 536-537.
 GAUMANN, E., 1950.—Principles of Plant Infection. Pp. 543. Crosby Lockwood and Son, Ltd., London.
 GREEN, D. E., 1934.—Antirrhinum Rust. A disease new to Great Britain. *J. R. hort. Soc.*, 59: 119-126.
 ———, 1941.—Antirrhinum Rust. IV. Improvement of rust-resistant varieties. *J. R. hort. Soc.*, 66: 83-86.
 HASSEBRAUK, K., 1937.—Zur Frage der Verbreitung des Löwenmaulrostes durch das Saatgut. *Blumen- u. Pfl. Bau ver. Gartenwelt*, 41: 261-262. Abs. in *R.A.M.*, 16: 752, 1937.
 JORSTAD, I., 1946.—Snapdragon rust and snapdragon mildew. Two newly introduced parasitic fungi. *Norg. Gart. Foren. Tidsskr.*, 36: 497-498. Abs. in *R.A.M.*, 26: 398, 1947.
 LAMBERT, E. B., 1929.—The relation of weather to the development of stem rust in the Mississippi Valley. *Phytopathology*, 19: 1-71.
 LEPIK, E., 1941.—Spread of snapdragon rust in Europe. *Int. Bull. Pl. Prot.*, 15: 93m.
 MAINS, E. B., 1924.—Notes on the life history of the snapdragon rust, *Puccinia antirrhini* Diet. and Holw. *Phytopathology*, 14: 281-287.*
 PALM, B. T., 1937.—*Puccinia antirrhini* Diet. et Holw. på Öland. *Svensk bot. Tidskr.*, 31: 288-289. Abs. in *R.A.M.*, 16: 679, 1937.
 PELTIER, G. L., 1919.—Snapdragon rust. *Univ. Ill. Agric. Exp. Sta. Bull.*, 221: 535-548.
 PRETI, G., 1935.—Una malattia dell' *Antirrhinum majus* L. nuova per la micologia italiana (*Puccinia antirrhini* Dietel e Holway). *Riv. Pat. veg.*, 25: 361-372. Abs. in *R.A.M.*, 15: 228, 1936.



Aeschnidiopsis flindersiensis (Woodward).



Bacteria from Macquarie Island.



Collenia frequens.